

TRINERVATE LEAVES, YELLOW FLOWERS, TAILED
ANTHERS, AND POLLEN VARIATION IN
DISTEPHANUS CASSINI
(VERNONIEAE: ASTERACEAE)

Harold Robinson and Brian Kahn

Abstract.—The genus *Distephanus* Cassini is resurrected for a series of mostly western Indian Ocean and eastern African species of Vernonieae including the only members of the tribe having trinervate leaves and yellow flowers. The genus is characterized by distinct basal stylar nodes, sclerified basal appendages on the anther thecae, and a unique form of pollen. Twenty-six species are recognized in the genus, 24 being newly transferred, and additional possible members are listed.

The broad concept of *Vernonia* suffers from most of the ills of a core genus, being excessively paraphyletic, distracting from more appropriate phyletic comparisons between its parts and other genera of the tribe, and being defined primarily by what it is not rather than by what it is. Such concepts ultimately encourage shoddy taxonomy, and *Vernonia* is no exception, having come to include elements that do not even fit the broadest definition of the genus when examined critically.

It is by virtue of such lapses of careful study that the Paletropical genus *Distephanus* has fallen into the synonymy of *Vernonia*. *Distephanus* is a genus with predominantly yellow flowers in a tribe that otherwise lacks them, and the genus includes the only members of the tribe with trinervate leaves. Furthermore, the anther thecae of the genus are almost as prominently appendaged at their bases as those of the American genus *Piptocarpha* which is distinguished by that character.

Distephanus was first described by Cassini (1817) on the basis of a single species, *Conyza populifolia* Lam., from Mauritius. Cassini (1819) distinguished the genus by its pappus, described as 10 short outer squamellate scales alternating with 10 longer in-

ner linear-squamellate scales. His description mentioned the yellow-flowered heads, and a microfiche of the specimen in the Jussieu herbarium shows that the poplar-like leaves are trinervate. The claimed pappus distinction seems to have been ignored in subsequent literature as *Distephanus* has fallen into the synonymy of *Vernonia*, and the pappus was not mentioned by Humbert (1960) who related the yellow-flowered *Vernoniae* of Madagascar to the genus. The genus name has been transferred to sectional status by Bentham and Hooker (1873) for the single species, and to subsectional status by Jones (1981) for mostly unrelated species of Malayasia. With these latter exceptions, the name *Distephanus* has been ignored in recent literature.

It is the African members of the same group that were later segregated from *Vernonia* as the genus *Gongrothamnus* Steetz, a genus that was transferred to the Senecioneae by Bentham and Hooker (1873) on the basis of its yellow flowers and trinervate leaves. *Gongrothamnus* was reduced to synonymy under *Vernonia* by Hoffmann (1890-1894) at the same time that he named a new genus *Newtonia* in the same Senecioneae on the basis of still another species of the group from Angola. The name *Newtonia* was a

later homonym and a new name, *Antunesia* was provided by Hoffmann in 1893. Hoffmann (1902) ultimately corrected his error, recognizing *Gongrothamnus* at generic level and placing *Antunesia* in its synonymy. Brown (1909) briefly summarized some of the work in *Gongrothamnus*, but reduced it again to synonymy under *Vernonia*, being unaware of the importance of the trinervate leaves, and knowing no other character except the yellow flowers.

Almost all recent students of the Vernonieae have treated the yellow-flowered species as part of *Vernonia*. Wild (1978) placed the yellow-flowered species of the Zambezica area in *Vernonia* along with some trinervate species with reddish to purplish flowers. Humbert (1960) placed the yellow-flowered species of Madagascar in two groups with the note that the name *Distephanus* would apply to his Group V. Jones (1981) recognized the yellow-flowered species as a subsection of *Vernonia* in his classification of the Paletropical members of the genus, but as mentioned above, treated *Distephanus* as a distinct indirectly related subsection.

The retention of the name *Gongrothamnus* at the generic level by Robinson et al. (1980) was based on the difference in flower color along with the realization that subdivision of *Vernonia* seemed inevitable. A firm basis for the distinction of the yellow-flowered species has arisen from the present study initiated as a review of stylar nodes in the tribe. The nodes as well as the leaf trinervation, flower color, anther tails, endothelial cells, and pollen variation all indicate a distinctive element of small shrubby or scandent Vernonieae distributed primarily in the western Indian Ocean. The characters involved warrant the following individual analyses.

Trinervate leaves.—Early observations of *Gongrothamnus* by the senior author, and studies by most other authors (Humbert 1960, Wild 1978) were without recognition of the importance of the trinervate character

in the tribe. Only Bentham and Hooker (1873) seem to have appreciated how unusual the character is in the tribe when giving their reasons for transferring *Gongrothamnus* to the Senecioneae. Trinervation versus pinnate venation is certainly highly variable in most other tribes in the family, commonly varying within genera. It was only with more detailed studies of Neotropical Vernonieae that the senior author noted the fundamentally pinnate nature of leaf venation in the Vernonieae (Robinson et al. 1980) and commented upon the lack of trinervation in the tribe in comparisons with the Liabeae (Robinson 1983, Robinson et al. 1985). The species of *Distephanus* can now be seen as an exception in the Vernonieae, an exception in which most of the species are trinervate or have leaves reduced to an ill-defined venation pattern. Trinervation has been seen in no other Vernonieae and is regarded as uniquely derived in this Indian Ocean element of the tribe.

Yellow flowers.—Closely correlating with the trinervate leaves in the Vernonieae are the yellow flowers. The latter character is sufficiently exceptional in the tribe to have caused both Bentham and Hooker (1873) and Hoffmann (1890–1894) to place members of the genus in the tribe Senecioneae. A few species on the African mainland were noted by Wild (1978) as having trinervate leaves but not having yellow flowers. These are scandent like the yellow-flowered species of *Distephanus* on the mainland and have stylar nodes, basal appendages on the anther thecae, and mostly unstriated endothelial sclerified shields as in that genus. These reddish species appear to be members of *Distephanus*, but occur outside of the apparent center of distribution of the genus, where they seem to be a derived element. Since hybridization is common in the Asteraceae, such convergences in the Vernonieae may well represent borrowing of traits from the associated reddish-flowered Vernonieae on the continent. In any case, the character failure is regarded as a de-differentiation be-

tween two well-defined elements of the tribe and not a relict of any ancestral type.

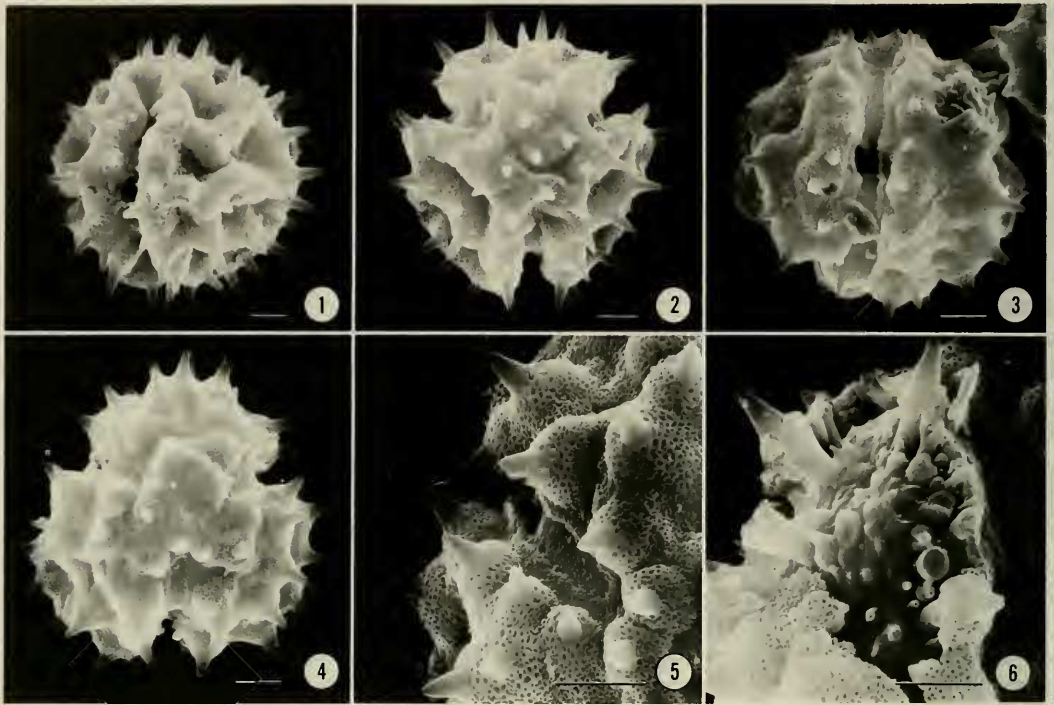
Basal appendages of the anther.—The Vernoniae, like almost all Cichorioideae, have spurred bases on the anthers, but in addition to the fertile extensions, most thecae have at least a fringe of sterile tissue at the lower end. In typical *Vernonia* and most species that have been placed in the genus, the sterile tissue is usually unsclerified and easily overlooked, but some species in basically unappendaged groups, such as *V. megaphylla* Hieron. have a small sclerified basal appendage. In Neotropical Vernoniae, prominent narrow sclerified basal appendages are the character by which *Piptocarpha* has traditionally been distinguished from *Vernonia*. In Paleotropical members of the tribe such as *Distephanus*, basal anther appendages have not been noted, probably because they usually are broad and do not have the form of a narrow tail. One African segregate of *Vernonia*, *Baccharioides* (*Vernonia* subgenus *Stengelia*), has no sclerified appendage, but all of *Distephanus*, typical *Gymnanthemum*, and some species of Humbert's (1960) Group IV from Madagascar show distinct basal appendages. A narrow basal appendage in the form of a broad tail does occur in *Distephanus glandulicincta*. The character technically places these elements outside of the traditional definition of *Vernonia*, even though the less obvious appendages of these African Vernoniae have traditionally been ignored. The appendages in *Gymnanthemum* and Group IV may indicate relationship of these groups to *Distephanus*, but other characters such as the trinervate leaves and flower color are different. Of these, only some species of Group IV have a distinct stylar node, but they differ by having deciduous inner bracts in the involucre.

Endothelial cells.—All members of *Distephanus* examined have median endothelial cells with a single unlined sclerified shield on the outer surface. These superficially appear like a series of non-contiguous

cells in the endothecium. This contrasts with the more annulated appearance of other Vernoniae that have been seen. A tendency toward an intermediate condition occurs in *D. angulifolius*, a species of continental Africa noted above for possible introgression with other Vernoniae in flower color. *Gymnanthemum* and Humbert's Group IV both can have sclerified shields approaching those of *Distephanus* in form but with multifid ends. Those of typical *Gymnanthemum* differ further in their frequently oblique or nearly transverse direction.

Apical anther appendages.—Glands occur on the apical anther appendages of typical *Vernonia* and on many other Neotropical species placed in the genus. Such glands are lacking in some of the American species which seem to have generally lost the ability to produce glands anywhere on the plant. The African groups seen in the present study show no glands on the appendages in any species, even when glands occur on other parts.

Stylar node.—An expanded node with sclerified cells at the base of the style occurs commonly in the Vernoniae, and the character may be basic to the tribe. The character is most common, however, in Neotropical members of the tribe; it has a comparatively restricted distribution among Paleotropical species. A few African entities such as *V. bainesii* Oliv. & Hiern, have slight nodal development, but distinct nodes as large as any in the tribe seem almost totally restricted to and characteristic of *Distephanus* among the Paleotropical Vernoniae. The mature node of *Distephanus* is puck-like, narrowing abruptly above into the stalk partly as a result of shrinkage of unsclerified stalk tissue. A few species from Madagascar placed by Humbert (1960) in his Group IV, such as *V. andrangovalensis* Humb. and *V. appendiculata* Less., have nodes as large, but the latter group differs by being larger shrubs and trees, having reddish flowers normal for the tribe, and having deciduous inner bracts of the involucre.

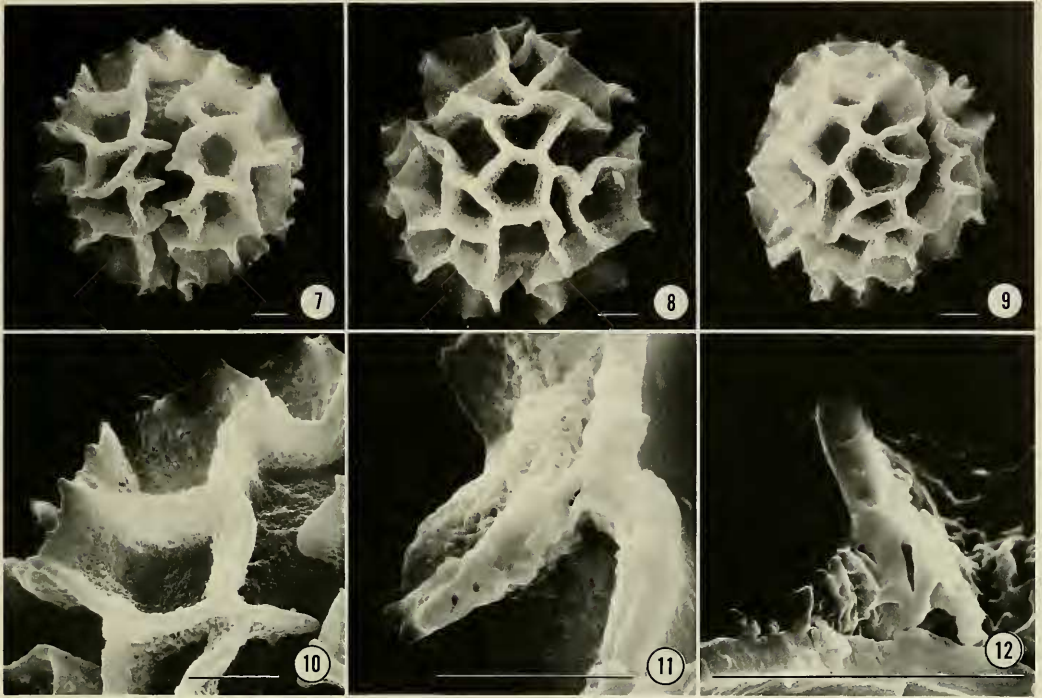


Figs. 1–6. Pollen of *Gymnanthemum* and *Distephanus*, lines = 5 μm . 1–2, *G. coloratum* (Willd.) R. & K., Equatorial and polar views showing sublophate intercolpar surface; 3–6, *D. divaricatus* (Steetz) R. & K., Colpar view; 4, Polar view, showing lack of regular sublophate intercolpar surface; 5, End of colpus; 6, Area of broken tectum showing basal columellae.

Pollen.—The so-called Lychnophora-type pollen (Stix 1960) or Type A pollen (Keeley and Jones 1979), the most widely distributed pollen type in the Vernoniaeae, is found in most species of *Distephanus* and in *Gymnanthemum* and Humbert's Group IV. The grains seen in *Distephanus* and Group IV are ca. 38–40 μm in diameter while those of typical *Gymnanthemum* ca. 45–47 μm in diameter. In *Distephanus* the Type A pollen occurs in all non-Madagascar species (Figs. 3–4) and six species seen from Madagascar, *D. antandroy*, *D. glandulicinctus*, *D. malacophytus*, *D. nummulariaefolius*, *D. rochonioides* and *D. subluteus*. The Type A pollen grains of *Distephanus* seem unusual in the irregularity of the surface pattern, an irregularity not seen in *Gymnanthemum* (Figs. 1–2) and believed here to be related to the irregularity seen in the surface pattern

of the non-Type A grains found in other species of *Distephanus*. Another aspect of these Type A grains that might be unusual shows in broken areas of *D. divaricatus* pollen, where separate smaller basal columellae occur in the spaces between the primarily basal columellae under the spines (Fig. 6).

Seven other species of *Distephanus* from Madagascar, *D. cloiselii*, *D. eriophyllus*, *D. mahafaly*, *D. mangokensis*, *D. ochroleucus*, *D. swinglei*, and *D. trinervis*, have a distinctive type of pollen not seen elsewhere in the tribe (Figs. 7–12). It is lophate with areolae distinct but lacking any definite order. The ridges are not pitted or perforated on the edges, but a weakly perforated tectum lines the lower sides and bottoms of the areolae (Fig. 10). The direct attachment of the crests to the foot layer seems intermittent within the area covered by perforated



Figs. 7–12. Pollen of *Distephanus ochroleucus* (Baker) R. & K., lines = 5 μm . 7, Colpar view; 8, Polar view; 9, Oblique view of intercolpar area showing irregular lophate pattern; 10, Areolae showing non-perforate edges of tectum ridges and perforate basal parts; 11–12, Broken sections of ridges showing parts with and without direct median attachment of the foot layer.

tectum. The pores are located in long colpi into which walls partially intrude in an alternating pattern (Fig. 7). The alternating pattern of the intruding walls seems characteristic and is apparently directly linked to the characteristic irregularity of the tectum areolation. The ridges of these species of *Distephanus* (Figs. 11–12) are reminiscent of those in the pollen of *Cyanthillium* Blume, *Phyllocephalum* Blume, *Stokesia* L'Her., or the Elephantopinae, but the latter have more regular reticulations, have more truncated colpi or complete cross-walls above and below the pores which interrupt any colpi, and have the ridges raised on a series of small columellae or a fenestrated curtain above the surface of the foot layer. None have the partial perforated tectum seen in *Distephanus*.

The presence of variation of pollen type

within the well defined related group *Distephanus* is not the first example of such variation in the Vernoniaceae. As in other examples, the variation involves the Type A pollen and is not a variation between two of the lophate types. This type of anomalous occurrence along with the general pattern of distribution of Type A in the tribe suggests that the Type A is often the product of reversion and not necessarily the primitive form. In this particular case, one can theorize that it is only necessary developmentally to limit the type of structure seen on the ridge margins to the isolated spine tips and allow the perforated tectum to become the continuous structure of the surface instead. In any case, the presence of Type A pollen is not regarded here as evidence of either primitiveness or direct relationship between the species in which it occurs. Con-

sidering the specialized lophate pollen of *Distephanus* alone seems to present a more realistic picture of relationship, with the type being restricted to the distinctive genus centered geographically in Madagascar.

Distephanus is a genus differing in two obvious characters from all other Vernoniaeae. All the species have either the yellow flowers or the trinervate leaves, neither feature occurring elsewhere in the tribe. The naturalness of the group is supported by other less obvious but nearly as unique features such as the puck-like stylar node, and the simple broad sclerified shields of the endothelial cells. The basal appendages of the anther thecae place *Distephanus* with *Gymnanthemum* and parts of Humbert's Group IV technically outside of the traditional definition of *Vernonia* to whose North American type they have only an extremely paraphyletic relationship. Species of *Distephanus* showing flower color or endothelial cells approaching the type seen in "*Vernonia*" are seen as recent introgressions. The genus *Distephanus* is resurrected and defined as follows.

Distephanus Cassini

Distephanus Cassini, Bull. Soc. Philom. 1817:151. 1817. Type *Conyza populifolia* Lam.

Vernonia sect. *Distephanus* (Cassini) Benth & Hooker f., Gen. Pl. 2:228. 1873.

Vernonia subsect. *Distephanus* (Cassini) Jones, Rhodora 83:68. 1981.

Gongrothamnus Steetz ex Peters, Reise Mossamb. Bot. 336. 1862. Type *Gongrothamnus divaricatus* Steetz.

Vernonia subsect. *Gongrothamnus* (Steetz) Jones, Rhodora 83:65. 1981.

Newtonia O. Hoffmann, Engler & Prantl., Natürl. Pflanzenfam. 4(4):285. 1892. Type *Newtonia angolensis* O. Hoffmann. Not *Newtonia* Baill. 1888.

Antunesia O. Hoffmann, nom. nov., Bolet. Soc. Brot. 10:178. 1893. Type *Newtonia angolensis* O. Hoffmann.

Small shrubs or vines. Leaves alternate, blades usually trinervate, often with truncate or subcordate bases, less often narrow with cuneate bases and irregularly pinnate venation. Inflorescences terminal on branches, of corymbose cymes, with minute bracts, peduncles short but distinct. Heads campanulate; involucre bracts mostly 21–24, ca. 75 in *D. forrestii*, persistent, multi-seriate, graduated, unappendaged apically; receptacle epaleaceous. Flowers mostly 10–16 in a head, ca. 75 in *D. forrestii*. Corollas usually yellow, purplish in a few continental African species; thecae of anthers with distinct broad sclerified basal appendages; endothelial cells with simple, broad, non-contiguous, sclerified shields; apical appendages of anthers without glands; style base with large abruptly broadened node. Achenes cylindrical to prismatic, sometimes subtriquetrous or quadrangular, with 5–12 ribs, usually 10, setulae or glands present or absent; carpopodium turbinate; pappus of 10 or more shorter outer squamellae alternating with 10 or more longer capillary or linear inner bristles or squamellae. Pollen in many species Type A with continuous intercolpar perforated tectum and subreticulately arranged spines, in some Madagascar species irregularly lophate with perforated tectum restricted to lower sides and bases of crests, with distinct colpi intruded upon by short alternating spurs of reticulate tectum.

The species recognized in the genus in this study are as follows:

Distephanus angolensis (O. Hoffmann) H. Robinson & B. Kahn, comb. nov.

Newtonia angolensis O. Hoffm., Natürl. Pflanzenfam. 4(5):285. 1892. *Antunesia angolensis* (O. Hoffm.) O. Hoffm., Bolet. Soc. Brot. 10:178. 1893. *Gongrothamnus angolensis* (O. Hoffm.) Hiern, Cat. Welw. Afr. Pl. 1:592. 1898. *Vernonia angolensis* (O. Hoffm.) N. E. Brown, Kew Bull. 1909: 116. 1909. SW Africa.

Distephanus anisochaetoides (Sond)

H. Robinson & B. Kahn, comb. nov.

Vernonia anisochaetoides Sond, *Linnaea* 23: 61. 1850. SE Africa.**Distephanus angulifolius** (DC.)

H. Robinson & B. Kahn, comb. nov.

Vernonia angulifolia DC., *Prodr.* 5:29. 1836. SE Africa.**Distephanus antandroy** (H. Humbert)

H. Robinson & B. Kahn, comb. nov.

Vernonia antandroy H. Humb., *Not. Syst. Paris* 8(1):7. 1939. Madagascar.**Distephanus cloiselii** (Moore)

H. Robinson & B. Kahn, comb. nov.

Vernonia cloiselii Sp. Moore, *Journ. Bot.* 44:145. 1906. Madagascar.**Distephanus divaricatus** (Steetz)

H. Robinson & B. Kahn, comb. nov.

Gongrothamnus divaricatus Steetz in Peters, *Reise Mossamb. Bot.* 2:342. 1864. Not *V. divaricatus* Swartz, 1806. *Gongrothamnus aurantiacus* O. Hoffm., *Bot. Jahrb.* 30:433. 1901. *Vernonia aurantiaca* (O. Hoffm.) N. E. Brown, *Kew Bull.* 1909:116. 1909. *Vernonia vitellina* N. E. Brown, *Kew Bull.* 1909:117. 1909. East Africa.**Distephanus eriophyllus** (Drake)

H. Robinson & B. Kahn, comb. nov.

Vernonia eriophylla Drake, *Bull. Soc. Bot. Fr.* 46:230. 1889. Madagascar.**Distephanus forrestii** (Anthony)

H. Robinson & B. Kahn, comb. nov.

Vernonia forrestii Anthony, *Notes Bot. Gard. Edinb.* 18:35. 1933. Yunnan.**Distephanus garnieriana** (Klatt)

H. Robinson & B. Kahn, comb. nov.

Vernonia garnieriana Klatt, *Linnaea* 37:508.1872. *Vernonia parviflora* (error for *parvifolia*) Klatt, *Ann. Sc. Nat.* 5^e sér. *Bot.* 362. 1873. *Vernonia lyallii* Baker, *J. Linn. Soc.* 20:174. 1883. *Vernonia moquioides* Baker, *J. Linn. Soc.* 20:177. 1883. *Vernonia alboviridis* Baker, *J. Linn. Soc.* 25:325. 1890. Madagascar.**Distephanus glandulicinctus** (H. Humb.)

H. Robinson & B. Kahn, comb. nov.

Vernonia glandulicincta H. Humb., *Not. Syst. Paris* 8(4):306. 1948. Madagascar.**Distephanus glutinosus** (DC.)

H. Robinson & B. Kahn, comb. nov.

Vernonia glutinosa DC., *Prodr.* 5:18. 1836. *Vernonia scariosa* Baker, *Journ. Bot.* 20: 169. 1882, hom. illeg. *Vernonia lepidophylla* Drake, *Bull. Soc. Bot. Fr.* 46:229. 1889. Madagascar.**Distephanus lastellei** (Drake)

H. Robinson & B. Kahn, comb. nov.

Vernonia lastellei Drake, *Bull. Soc. Bot. Fr.* 46:232. 1899. *Vernonia goudotii* Drake, *Bull. Soc. Bot. Fr.* 46:239. 1899. Madagascar.**Distephanus mahafaly** (H. Humb.)

H. Robinson & B. Kahn, comb. nov.

Vernonia mahafaly H. Humb., *Not. Syst. Paris* 8(1):10. 1939. Madagascar.**Distephanus majungensis** (H. Humb.)

H. Robinson & B. Kahn, comb. nov.

Vernonia majungensis H. Humb., *Not. Syst. Paris* 13:308. 1948. Madagascar. Lectotype designated here, *Humbert & Perrier 2117* (P).**Distephanus malacophytus** (Baker)

H. Robinson & B. Kahn, comb. nov.

Vernonia malacophyta Baker, *Journ. Linn. Soc.* 25:323. 1890. *Vernonia rampans*

- Baker, Journ. Linn. Soc. 25:323. 1890. *Vernonia grandidieri* Drake, Bull. Soc. Bot. Fr. 46:240. 1899. Madagascar.
- Distephanus manambolensis*** (H. Humb.) H. Robinson & B. Kahn, comb. nov.
- Vernonia manambolensis* H. Humb., Not. Syst. Paris 13:306. 1948. Madagascar.
- Distephanus mangokensis*** (H. Humb.) H. Robinson & B. Kahn, comb. nov.
- Vernonia mangokensis* H. Humb., Bull. Soc. Bot. Fr. 87:347. 1940. Madagascar.
- Distephanus nummulariaefolius*** (Klatt) H. Robinson & B. Khan, comb. nov.
- Decaneurum* (*Gymnanthemum*) *nummulariaefolium* Klatt, Ann. Sc. Nat. 5^e sér. Bot. 18:363. 1873. *Gongrothamnus multiflorus* Klatt, Flora 68:205. 1885. *Vernonia leucolepis* Baker, Journ. Bot. 25:322. 1890. Madagascar.
- Distephanus ochroleucus*** (Baker) H. Robinson & B. Kahn, comb. nov.
- Vernonia ochroleuca* Baker, Journ. Linn. Soc. 20:179. 1885. *Vernonia trichantha* Baker, Journ. Linn. Soc. 21:416. 1884. Madagascar.
- Distephanus polygalaefolia*** (Less.) H. Robinson & B. Kahn, comb. nov.
- Vernonia polygalaefolia* Less, Linnaea 6:628. 1831. *Vernonia arbutifolia* Baker, J. Bot. 20:169. 1882. *Vernonia perrieri* Drake, Bull. Soc. Bot. Fr. 46:229. 1899. Madagascar.
- Distephanus populifolius* (Lamarck) Cassini
- Conyza populifolia* Lamarck, Encyc. 2:87. 1786. *Distephanus populifolius* (Lamarck) Cassini, Bull. Soc. Philom. 1817:151. 1817. *Vernonia populifolia* (Lamarck) Spreng., Syst. 3:434. 1826. Mauritius.
- Distephanus rochonoides*** (H. Humb.) H. Robinson & B. Kahn, comb. nov.
- Vernonia rochonoides* H. Humb., Bull. Soc. Bot. Fr. 87:346. 1940. Madagascar.
- Distephanus streptocladus*** (Baker) H. Robinson & B. Kahn, comb. nov.
- Vernonia streptoclada* Baker, Journ. Linn. Soc. 21:416. 1885. Madagascar.
- Distephanus subluteus*** (S. Elliot) H. Robinson & B. Kahn, comb. nov.
- Vernonia sublutea* S. Elliot, Journ. Linn. Soc. 29:26. 1891. Madagascar.
- Distephanus swinglei*** (H. Humb.) H. Robinson & B. Kahn, comb. nov.
- Vernonia swinglei* H. Humb., Not. Syst. Paris 8(1):8. 1939. Madagascar.
- Distephanus trinervis* Boj. ex DC.
- Distephanus trinervis* Boj. ex DC., Prodr. 5:75. 1836. *Distephanus capitatus* Boj. ex DC., Prodr. 5:74. 1836. *Vernonia capitata* (Boj. ex DC.) Drake in Grandidieri, Hist. Madag. Pl. VI, Atlas, pl. 464. 1897. *Vernonia trinervis* (Boj. ex DC.) Drake, Bull. Soc. Bot. Fr. 46:228. 1899. *Vernonia rusillonii* Hochr., Ann. Cons. Genève, 11-12:117. 1908. Madagascar.
- Additional species having the characters of the genus according to Humbert (1960) but not seen in this study are as follows: *Vernonia ambongensis* H. Humb., *V. bara* H. Humb., *V. bakeri* Vatke, *V. capuronii* H. Humb., *V. Grevei* Drake, *V. ibityensis* H. Humb., *V. madagascariensis* Less., *V. poissonii* H. Humb., *V. polytricholepis* Baker, *V. quartziticola* H. Humb., *V. rhodopappa* Baker, *V. spiciforma* Klatt.
- In the course of the present study it has seemed best to recognize *Gymnanthemum* at the generic level also, since it also falls outside of the definition of traditional *Vernonia*, and the status is inevitable in any

final revision of the tribe. This would not be so important at the present time except for the fact that the oldest name for the type species *G. cupulare* Cass. has never been transferred to the genus. There seems to be no reason for the precedence usually given to the Persson name *Baccharis senegalensis* since the Willdenow name antedates it by four years, unencumbered by inadequate description or homonymy.

***Gymnanthemum coloratum* (Willd.) H. Robinson & B. Kahn, comb. nov.**

Eupatorium coloratum Willd., Sp. Pl. 3: 1768. 1803.

Acknowledgments

The photographs of the pollen were prepared by the Smithsonian Institution Museum of Natural History SEM laboratory supervised by Walter Brown. An Hitachi 570 scanning electron microscope was used. The microscope was operated by Heidi Wolf. Dr. Joan Nowicke is thanked for use of the facilities of the Palynological Laboratory in the Smithsonian Department of Botany.

Literature Cited

- Bentham, G., and Hooker, J. D. 1873. —Genera Plantarum 2(1):1–554.
- Brown, N. E. 1909. List of plants collected in Ngamiland and northern part of the Kalahari Desert, chiefly in the neighbourhood of Kwebe and along the Botletle and Lake rivers.—Kew Bulletin of Miscellaneous Information 1909:89–146.
- Cassini, H. 1816–1817. Aperçu des genres nouveaux dans la famille des Synanthérées.—Bulletin de la Société Philomatique 1816:198–200; 1817: 10–13, 31–34, 66–70, 115–118, 137–140, 151–154.
- . 1819. Distéphane. In G. Cuvier, ed., Dictionnaire des Sciences Naturelles 13:361.
- Hoffmann, O. 1890–1894. Compositae. In A. Engler and K. Prantl, ed., Die Natürlichen Pflanzenfamilien 4(5):87–387. Leipzig.
- . 1893. Compositae de Africa portugueza.—Boletim da Sociedade Broteriana 10:170–185. “1892.”
- . 1902. Compositae. In Engler, A., Berichte über die botanischen Ergebnisse der Nyassa-See und Kinga-Gebirgs-Expedition der Hermann- und Elise-geb. Heckmann-Wentzel-Stiftung. IV. Die von W. Goetze am Rukwu-See und Nyassa-See sowie in den zwischen beiden Seen gelegenen Gebirgsländern insbesondere dem Kinga-Gebirge gesammelten Pflanzen, nebst eigenen Nachträgen (durch bezeichnet) zu Bericht III.—Botanische Jahrbücher 30:421–445.
- Humbert, H. 1960. 189° Famille Composées (Compositae) Tome 1.—Flore de Madagascar et des Comores (Plantes vasculaires) 1:1–338.
- Jones, S. 1981. Synoptic classification and pollen morphology of *Vernonia* (Compositae: Vernoniaeae) in the Old World.—Rhodora 83:59–75.
- Keeley, S., and Jones, S. B. 1979. Distribution of pollen types in *Vernonia* (Compositae).—Systematic Botany 4:195–202.
- Robinson, H. 1983. A generic review of the tribe Liabeae (Asteraceae).—Smithsonian Contributions to Botany 54:1–69.
- , Bohlmann, F., and King, R. M. 1980. Chemosystematic notes on the Asteraceae. III. Natural subdivisions of the Vernoniaeae.—Phytologia 46:421–436.
- , Powell, A. M., King, R. M., and Weedin, J. F. 1985. Chromosome numbers in Compositae, XV: Liabeae.—Annals of the Missouri Botanical Garden 72:469–479.
- Stix, E. 1960. Pollenmorphologische untersuchungen an Compositen.—Grana Palynologica 2(2):41–104, pl. 1–21.
- Wild, H. 1978. The Compositae of the Flora Zambesiaca Area 8. Vernoniaeae (*Vernonia*).—Kirkia 2:31–127.

Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.